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The prey captured by web building spiders (Araneae: Linyphiidae) in comparison with feeding experiments

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The prey captured by web building spiders (Araneae: Linyphiidae) in comparison with feeding experiments. - Three linyphiid spiders, *Frontinellina frutetorum* (C.L. Koch), *Neriene radiata* (Walckenaer) and *Linyphia triangularis* Clerck were studied in an area of forest regrowth in Eastern Austria. *F. frutetorum* and *N. radiata* were both active in spring and early summer, but utilised significantly different vegetation heights for web placement, while *L. triangularis* only emerged in late summer. In addition to these spatial and temporal differences, each spider species utilised a different prey spectrum. *N. radiata* captured more Sciaridae (Diptera) than expected while *L. triangularis* subdued more Myrmicinae (Hymenoptera) than expected. A feeding experiment using Sciaridae, Aphidina (Homoptera), Myrmicinae and Drosophilidae (Diptera) as prey was conducted to see if differences in attack efficiency are responsible for the observed variation in prey capture. However, there was no significant difference in the number of prey items successfully captured by the spiders during the experiment. In addition to feeding experiments, the potential prey available to the spiders, sampled by sticky traps at different times of the season as well as at different vegetation heights, according to the spiders' spatial and temporal distribution, were compared. The results indicate that insect abundance varies with season as well as throughout different vegetation strata. Consequently, it seems more likely that species specific prey capture efficiency has little influence on prey capture and that insect availability governed the observed prey capture patterns for these spiders.

Key-words: *Frontinellina frutetorum* - *Neriene radiata* - *Linyphia triangularis* - prey capture - feeding experiment.

INTRODUCTION

The foraging success of any predator depends on its ability to find and successfully subdue prey. Spiders are usually described as generalist predators, although notable exceptions of prey specialists, such as the bola spider (*Mastophora* sp.) or the

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spider eating *Ero* sp., exist (FOELIX 1992). The predatory behaviour of web building spiders involves placing and constructing the web, subduing prey entangled in the web and ingestion (LEBORGNE *et al.* 1991).

For successful prey capture, any potential prey item must move in the vicinity of the web, must be unable to avoid coming into contact with the web and must be retained long enough for the spider to attack it (TURNBULL 1960). Once entangled in the web, some insects successfully employ a number of defence mechanisms such as a thick cuticle, aggressive behaviour (NENTWIG 1987) or chemical deterrents (EISNER & DEAN 1976) to counteract the attack of spiders. Furthermore, a spider can choose to attack or reject a given prey item, reflecting some kind of preferences (RIECHERT & LUCZAK 1982; TURNBULL 1973).

In view of the complex nature of prey capture, it is not surprising to find differences in the prey captured by various web building spiders (eg. ALDERWEIRELDT 1994; HERBERSTEIN & ELGAR 1994; MALT *et al.* 1990; NYFFELER *et al.* 1989; PASQUET & LEBORGNE 1990; WISE 1993). However, it is often difficult to relate any differences in prey capture to species specific variations in foraging behaviour.

Differences in the types of prey captured by three sympatric sheet web building spiders, *Frontinellina frutetorum* (C. L. Koch), *Neriene radiata* (Walckenaer) and *Linyphia triangularis* Clerck are reported here. An attempt is made to relate these prey capture patterns to species specific variations in prey capture efficiency and to differences in prey availability.

MATERIALS AND METHODS

The study was conducted in a mixed deciduous forest located in Eastern Austria near Hartberg (Styria). The study site consisted of an area of forest regrowth and the spiders constructed their sheet webs on the numerous young fir trees planted (HERBERSTEIN 1995).

F. frutetorum and *N. radiata* overlapped in their development, maturing concurrently in early summer. While both were frequently found on the same fir trees, the spiders utilised different vegetation layers, *F. frutetorum* selecting higher canopy and *N. radiata* lower canopy for web construction. In contrast, *L. triangularis* was seasonally isolated, maturing in autumn (HERBERSTEIN 1995).

The prey captured by *F. frutetorum* and *N. radiata* was sampled from May to July 1993 and from August to September 1993 for *L. triangularis*. Only those items on which the spiders were feeding were removed from the webs and later identified. The webs were surveyed at 1 to 2 hour intervals covering the spiders' entire foraging period.

The potential prey available to the spiders was estimated by trap captures. The traps consisted of transparent plastic sheets (30 cm by 30 cm) and were evenly covered on one side with a clear and water proof insect glue (Rotor Raupenleim). Traps were erected randomly at intervals of 30 cm from 0 to 180 cm. The traps were only exposed during periods when the webs were also surveyed and all items captured were removed and later identified.

A feeding experiment was conducted from 09 - 14 May 1994 using *F. frutetorum* and *N. radiata* and from 07 - 17 July 1994 using *L. triangularis*. Spiders were collected in the study area and released in the laboratory onto artificial, three-dimensional structures (height: 30 cm, maximum length and width: 30 cm) providing sufficient support for web construction. The experiment commenced after a total hunger period of 48 hours. Four prey types were tested: Aphidina (aphids), Sciaridae (nematoceran flies) and Myrmicinae (ants), collected from the investigation area as well as Drosophilidae (*Drosophila sp.*, fruit flies) from laboratory stock.

Each prey item was introduced into the web precisely above the spider and attack behaviour as well as prey capture was monitored. Attack behaviour was considered any rapid movement towards the prey along with plucking threads or shaking the entire web. The item was considered captured when the spider was holding it with the chelicerae.

The time taken until prey capture was measured in seconds. Any captured item was immediately removed and the second prey type was tested after a period of 30 minutes. The order at which the prey types were fed was random. Twenty spiders of each species were used and confronted only once with any given prey type.

Analysis

The prey spectra captured by the three spider species were compared using Hierarchical log linear tests. This analysis only considered prey types sampled at frequencies greater than 5%. The test also calculated standard residuals (z - values) with 95% confidence intervals at $\pm$ 1.96 to reveal which of the individual insect prey group frequencies differed.

Differences in the distribution and abundance of potential insect prey (trap captures) were also analysed using Hierarchical log linear tests. Trap data sampled at different vegetation heights (0 - 60 cm, 61 - 120 cm, 121 - 180 cm) and at different times of the season (May - July vs August - October) were compared. Trap data analyses considered prey types sampled at frequencies greater than 5% but also included the major prey types utilised by the spiders even if trap capture frequencies were less than 5%.

The numbers of prey items attacked and successfully captured by each spider species during the feeding experiment were analysed with χ^2 tests. The spiders' capture times measured during the feeding experiment for Aphidina, Sciaridae and Drosophilidae were compared using Kruskal-Wallis tests.

RESULTS

A total of 151 prey items were collected from the webs of *F. frutetorum*, 82 items from the webs of *N. radiata* and 138 from webs of *L. triangularis*. Aphidina, Cicadellidae (Homoptera), Sciaridae and Myrmicinae made up the major prey types amongst other insect groups of minor frequencies (Fig. 1). A comparison of prey spectra revealed significant differences (χ^2 = 54.5, df = 6, $P < 0.01$), as *N. radiata*

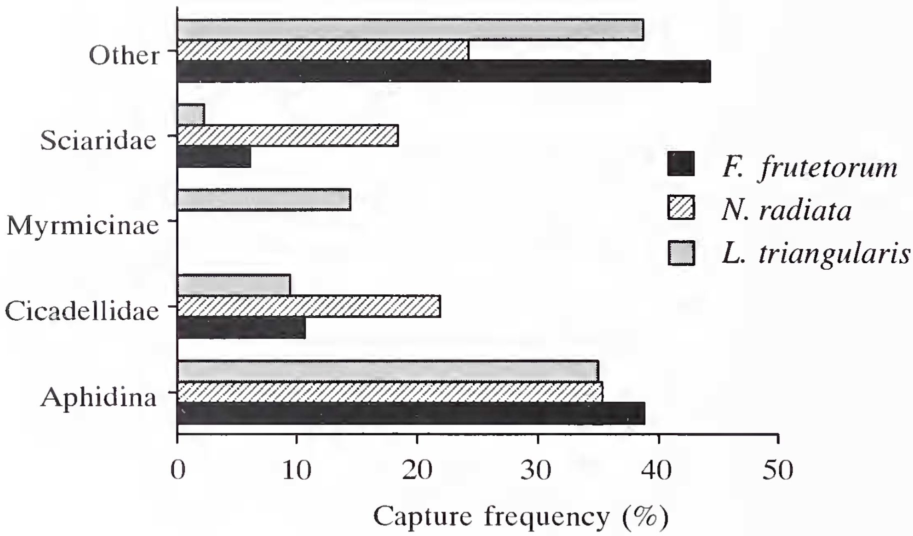

FIG. 1

The frequency distributions of insect prey captured in the field by *F. frutetorum*, *N. radiata* and *L. triangularis*.

captured more Sciaridae than expected, while *L. triangularis* captured more Myrmicinae than expected (Fig. 2).

The numbers of Aphidina, Sciaridae, Myrmicinae and Drosophilidae successfully captured (Tab. 1) by each spider species during the feeding experiment were similar ($\chi^2 = 9.0$, df = 6, $P > 0.05$). There was also no difference in the number of prey items that elicited an attack, irrespective of whether the item was subsequently captured or not (Tab. 2) ($\chi^2 = 0.723$, df = 6, $P > 0.05$). The median attack time (Tab. 3) it took to subdue Aphidina ($H = 7.5$, df = 2, $P < 0.05$) as well as Drosophilidae ($H = 10.9$, df = 2, $P < 0.01$) differed between the three spider species, while no significant difference was observed for the time taken to subdue Sciaridae ($H = 1.6$, df = 2, $P > 0.05$).

TABLE 1

The number of prey items successfully captured by *F. frutetorum*, *N. radiata* and *L. triangularis* during the feeding experiment.

	F. frutetorum	*N. radiata*	*L. triangularis*
Aphidina	14	17	12
Myrmicinae	0	0	3
Sciaridae	11	18	8
Drosophilidae	10	13	8

TABLE 2

The number of prey items attacked by *F. frutetorum*, *N. radiata* and *L. triangularis* during the feeding experiment.

	F. frutetorum	*N. radiata*	*L. triangularis*
Aphidina	16	18	14
Myrmicinae	12	17	14
Sciaridae	18	20	14
Drosophilidae	16	17	14

TABLE 3

First quartile, median and third quartile of the time (seconds) taken until successful prey capture by *F. frutetorum*, *N. radiata* and *L. triangularis*.

	F. frutetorum	*N. radiata*	*L. triangularis*
Aphidina	$Q_1 = 105$ $Q_2 = 360$ $Q_3 = 922.5$ $n = 13$	$Q_1 = 150$ $Q_2 = 630$ $Q_3 = 840$ $n = 14$	$Q_1 = 38$ $Q_2 = 142.5$ $Q_3 = 238$ $n = 12$
Sciaridae	$Q1 = 3$ $Q_2 = 3.5$ $Q_3 = 30$ $n = 10$	$Q1 = 2.5$ $Q_2 = 4$ $Q_3 = 5$ $n = 17$	$Q1 = 2$ $Q_2 = 2$ $Q_3 = 240$ $n = 8$
Drosophilidae	$Q1 = 3$ $Q_2 = 5$ $Q_3 = 10$ $n = 7$	$Q1 = 2$ $Q_2 = 2$ $Q_3 = 6$ $n = 11$	$Q1 = 1$ $Q_2 = 1$ $Q_3 = 2$ $n = 8$

The comparison of trap data revealed significant variations in the seasonal abundance as well as the vertical distribution of insects. The insect prey sampled in early summer (May - July) was significantly different to that sampled in autumn (August - October) ($\chi^2 = 99.2$, df = 9, $P < 0.01$) (Fig. 3). Similarly, the composition of insects sampled from May to July differed throughout the three height classes ($\chi^2 = 220.1$, df = 10, $P < 0.01$) (Fig. 4).

DISCUSSION

The main prey types captured by the spiders in the field were Aphidina, Sciaridae, Cicadellidae and Myrmicinae (Fig. 1). Consequently, the prey types tested in the feeding experiments reflect the importance of naturally captured prey. While Aphidina and Sciaridae were easily found and collected for the experiment, Cicadellidae were difficult to locate and capture and could not be tested. Drosophilidae were fed to see how spiders reacted to a novel prey type which was rarely captured

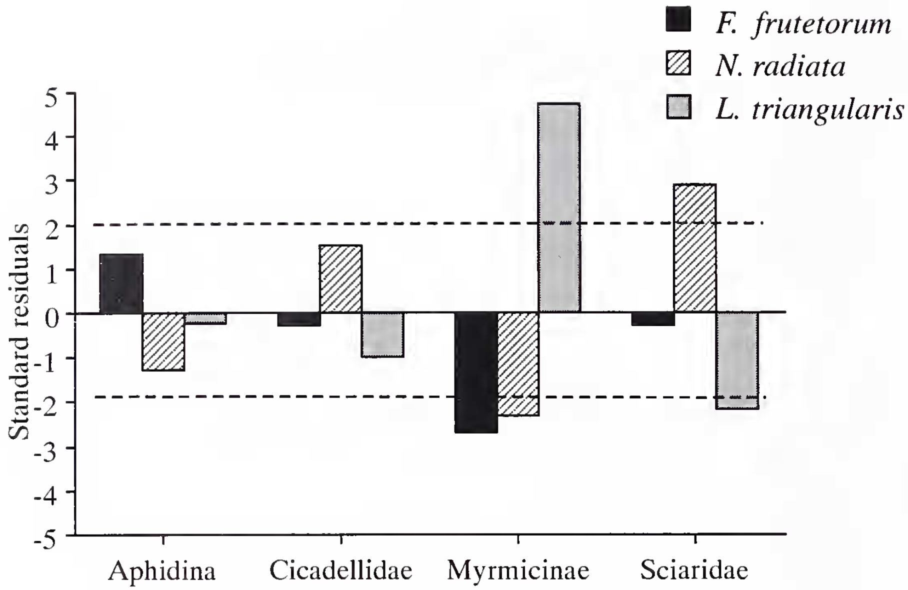

FIG. 2
The standard residuals and 95% confidence limits (- - - -) of the frequency distributions for prey items captured in the field by *F. frutetorum*, *N. radiata* and *L. triangularis*.

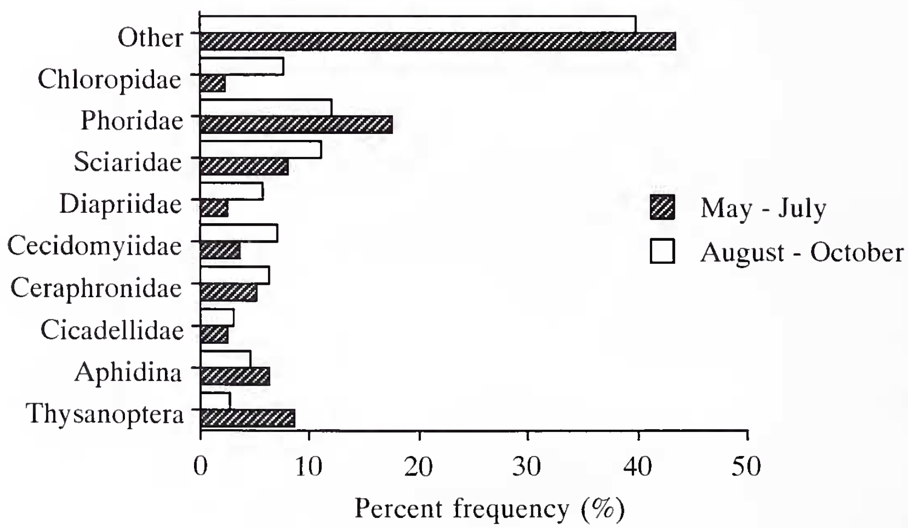

FIG. 3
The frequency distributions of prey sampled by the traps from May until July (total number of insects captured = 1184) and August until October (total number of insects captured = 717).

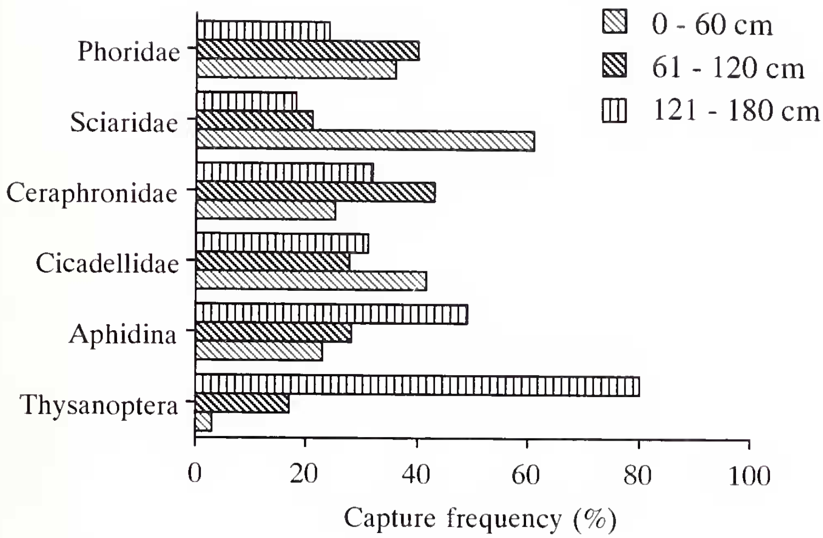

FIG. 4

The frequency distributions of prey sampled by the traps from May to July (total number of insects captured = 1184) at three different height classes (0 - 60 cm, 61 - 120 cm, 121 - 180 cm).

under natural conditions. Additionally, the Myrmicinae captured by the spiders in the field were all winged males and females, however, for the feeding experiment only workers were available and tested.

The feeding experiment was designed to investigate the spiders' reaction towards prey in the web. Other possible influences on prey capture success such as web visibility (CRAIG 1988; 1990; CRAIG & FREEMAN 1991) or attractive properties (CRAIG & BERNARD 1990; CRAIG & EBERT 1994) were not considered and the results should, therefore, be viewed within this context.

The results of the feeding experiment suggest that species specific capture efficiency of prey introduced into the web does not seem to have a major influence on prey capture success. *N. radiata* did not capture significantly more Sciaridae and *L. triangularis* did not subdue more Myrmicinae as suggested by field data.

Interestingly, species specific differences in attack time for Aphidina and Drosophilidae did not reflect in the number of items captured during the experiment. Moreover, although *N. radiata* captured more Sciaridae in the field, capture time for Sciaridae during the experiment was similar for all three spider species.

These results are in contrast to a similar approach (NENTWIG 1983), where the results of the feeding experiment reflected those of actual prey capture. In contrast to the present study, however, tests of significance were not conducted and prey data collected from various linyphiid and theridiid spiders were pooled.

The types of vibrations produced by an item in the web can provide important information about the profitability of prey and can potentially aid in preventing the spider from wasting energy in unprofitable pursuit (RIECHERT & LUCZAK, 1982; UETZ & HARTSOCK 1987). Yet, all prey types were initially attacked in similar proportions (Tab. 2), suggesting that Aphidina, Sciaridae, Myrmicinae and Drosophilidae were all judged worth an attack. The extent of the attack did, however, vary considerably possibly reflecting the expected prey profitability.

It is recognised that the width of the actual prey capture will depend on the availability of potential prey (NENTWIG 1987). As *F. frutetorum*, *N. radiata* and *L. triangularis* were distributed distinctly in terms of time of the season and web height, the analyses of the potential prey considered variations in the seasonal and vertical distribution, which differed significantly. However, the difficulties with estimating the total prey availability are recognised (CASTILLO & EBERHARD 1983; NENTWIG 1989). Using sticky traps to sample potential prey was probably more appropriate than other methods such as colour traps, which may attract insects from higher vegetation layers, or sweep nets, which are very distructive. Additionally, statistical analyses could not control for any possible variation caused by individual webs or traps. Therefore, trap data only indicate general trends, and should be interpreted with caution.

Despite these possible biases, the present results indicate that specific capture efficiency does not seem to influence prey capture success and that variations in prey supply is more likely to govern the actual prey captured by the spiders in accordance with other studies (CHACON & EBERHARD 1980; MCREYNOLDS & POLIS 1987; UETZ *et al.* 1978).

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